EFFECTS OF DENSITY, BEECH CROP AND WINTER FEEDING ON SURVIVAL OF JUVENILE GREAT TITS; AN ANALYSIS OF KLUYVER'S REMOVAL EXPERIMENT

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ABSTRACT Density dependent processes and the availability of food may play an important role in the determination of population size. To investigate the relationship between density and local survival of juvenile Great Tits *Parus m. major* Kluyver removed first brood fledglings in two years. An analysis is presented of the effects of this removal experiment, beech crop and additional feeding in winter on local survival. Beech-crop index was positively correlated with local survival of both first- and second-brood fledglings. Additional feeding in winter affected local survival of first, but not of second-brood fledglings. The effect of the removal experiment differed between birds fledging early or late in the season. Removal of first-brood fledglings had a negative effect on local survival of the remaining first-brood fledglings. This effect was in accordance with the (quadratic) relationship between density and survival found in control years, indicating that the relationship is causal. This is a destabilizing density dependent process. Possible underlying mechanisms are discussed. Removal of first-brood fledglings enhanced local survival of second-brood fledglings. The enhancement was in accordance with the relationship found in control years, indicating that this relationship too is causal. Density of second-brood fledglings did not affect local survival of first or second-brood fledglings. This study confirms that food and density-dependent processes play an important role in the determination of population size but the effect of these factors differs between birds fledging early or late in the season.

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INTRODUCTION

Density dependent processes and the availability of food have always been considered to play a major role in the determination of population size and have therefore received much attention in population biology (Kluyver 1971, Newton 1980, Cavé & Visser 1985). In this paper I will concentrate on the effects of density and availability of food in winter on the survival on juvenile Great Tits.

Density dependent survival has been documented in several tit species, e.g. Willow Tit *Parus montanus* (Ekman *et al.* 1981, Ekman 1984) and the Blue Tit *P. caeruleus* (Dhondt *et al.* 1990). In the Great Tit local survival of fledglings has been found to correlate with fledgling density in two studies (Dhondt 1971, McCleery & Perrins 1985) but not in another (Van Balen 1980). When first- and second-brood fledglings are analyzed separately it was found that local survival of second-brood fledglings is negatively correlated with density of first-brood fledglings (Kluyver 1971, Tinbergen *et al.* 1985) but survival of first-brood fledglings was not dependent on fledgling density. However, density of first-brood fledglings correlates well with density of breeding pairs and this may be the cause of the relationship found. Other, unidentified, factors may also be involved. Experiments, in which the density of fledglings is manipulated, are required to establish whether a causal relationship exists.

Local survival rate of second-brood fledglings is lower than that of first-brood fledglings (Kluyver 1951, Dhondt & Hublé 1968), and local survival rate

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of late fledglings is generally lower than that of early fledglings (Perrins 1965, Verhulst & Tinbergen 1991, but see Tinbergen & Daan 1990). Kluyver hypothesized that this was caused by competitive exclusion of the second-brood fledglings by the first-brood fledglings (Kluyver 1971). This idea is supported by the fact that second-brood fledglings are subdominant to first-brood fledglings in the first months of their lives (Drent 1983, p. 108) and by a demonstration of the effect of prior occupancy on dominance (Sandell & Smith 1991). Kluyver (1971) conducted an experiment to test his hypothesis. In two successive years he removed most of the first brood young before fledging. His analysis consisted of a comparison of the annual local survival rates of first and second-brood fledglings within control and experimental years. In control years, local survival of second-brood fledglings was lower than survival of first-brood fledglings but in the experimental years survival rate of first- and second-brood fledglings was approximately equal. He therefore concluded that density of first-brood fledglings has a negative effect on local survival of second-brood fledglings. In his analysis he assumed that the removal experiment did not affect survival of first-brood fledglings. However, the removal experiment also affected local survival of first-brood fledglings (see below). Kluyver also showed that adult density is negatively correlated with fledgling survival. In this analysis beech-crop index, with which local survival is associated (Perrins 1965, Van Balen 1980, Tinbergen *et al.* 1985), was not taken into account. This may affect his conclusions since there is a negative correlation between beech-crop index and adult density (Van Balen & Hage 1989). I therefore reanalyzed Kluyver's data with the aim to test his hypothesis that local survival of second-brood fledglings is causally related to density of first-brood fledglings. In addition the effect of fledgling density on the local survival of first-brood fledglings was analyzed.

The availability of food in winter has been shown to affect local survival rates of Great Tits (Perrins 1965, Von Haartman 1973, Van Balen 1980, Källander 1981, Tinbergen *et al.* 1985). I therefore also analyzed the effects on local survival of the size of the beech crop and the amount of additional feeding in winter.

METHODS

Kluyver conducted the experiment in 1967 and 1968 in De Hoge Veluwe, a mixed forest near Arnhem, The Netherlands, the study area covering 320 ha in this period. Nestboxes were checked weekly during the breeding season, all nestlings were ringed and most parents were caught and ringed (see Van Balen 1973) for details concerning the study area and procedures of data collection in the breeding season).

Density of first-brood fledglings was reduced by approximately 90% in 1967 and 80% in 1968. This was achieved through removal of all eggs or nestlings from most nests. In the first year most removals were in the egg phase, in the second year most removals took place in the nestling-phase.

I analyzed the annual local survival rates of first- and second-brood fledglings with a stepwise forward multiple regression procedure. Local survival was defined as recaptured within the study area after the 31st of March of the year following the year of fledging. Prior to analysis the local survival rates were arcsine transformed (Sokal & Rohlf 1969). The period 1960-71 was selected for the analysis because exactly the same study area was used during these years. Consequently, there were ten control years (1960 - 1966 and 1969 - 1971) and two experimental years (1967 & 1968).

The effect of additional feeding was investigated by including the amount of feeding as a variable in the multiple regression analysis (no feeding = 0, small scale feeding = 1, large scale feeding = 2). There was no additional feeding in winters following the years 1960-63, small scale feeding in 1964 and 1965 and large scale feeding in 1966-71 (Van Balen 1980).

Variables tested in the model are: beech-crop index of the autumn following the corresponding breeding season (figures taken from Bastide & Van Vredenburgh, 1970, and Van Balen 1980), the experiment as a dummy variable (control years = 0,

experimental years = 1), density of first- and second-brood fledglings, density of breeding adults and the amount of additional feeding in winter. Density is defined as birds per 10 ha.

In most years, density of second-brood fledglings and density of all late fledglings (hatched after 11 June) is nearly identical. The experimental years are an exception however, since breeding pairs of which the first clutch was removed often renested and their young were allowed to fledge. Most young from these repeat clutches fledged at approximately the same time as the second-brood fledglings and in experimental years the density of all late fledglings is therefore markedly higher than density of second-brood fledglings. This holds also for first-brood fledglings and early fledglings (hatched before 12 June), although the difference is much smaller. For this reason I also investigated the effect on local survival of density of all early and all late fledglings instead of first- and second-brood fledglings.

RESULTS

First-brood fledglings

Local survival rate of first-brood fledglings was positively correlated with beech-crop index (R^2 = 0.65, $P < 0.002$, Fig. 1a). To test whether the density-manipulation affected local survival rate, the experiment was added to this regression model as a dummy variable. Local survival in experimental years was lower than expected on the basis of the beech-crop index (Fig. 1a) although not significantly so ($R^2 = 0.70$, beech crop: $P < 0.002$, experiment: $P > 0.2$). When the residuals of the correlation with beech-crop index are plotted against density of first-brood fledglings (Fig. 1b), it can be seen that a quadratic relationship emerges. This relationship is significant in a multiple regression analysis (R^2 = 0.89, beech crop: $P < 0.002$, density: $P < 0.004$, density squared: $P < 0.004$). To test whether the significance of this relationship depended on the experimental years I repeated the analysis without the experimental years. Within this subset the relationship is still significant (R^2 = 0.91, beech crop: $P < 0.02$, density: $P < 0.02$, density squared: $P < 0.02$). Furthermore, the survival rates in the experimental years are in accordance with values expected on the basis of the control years (Fig. 1b).

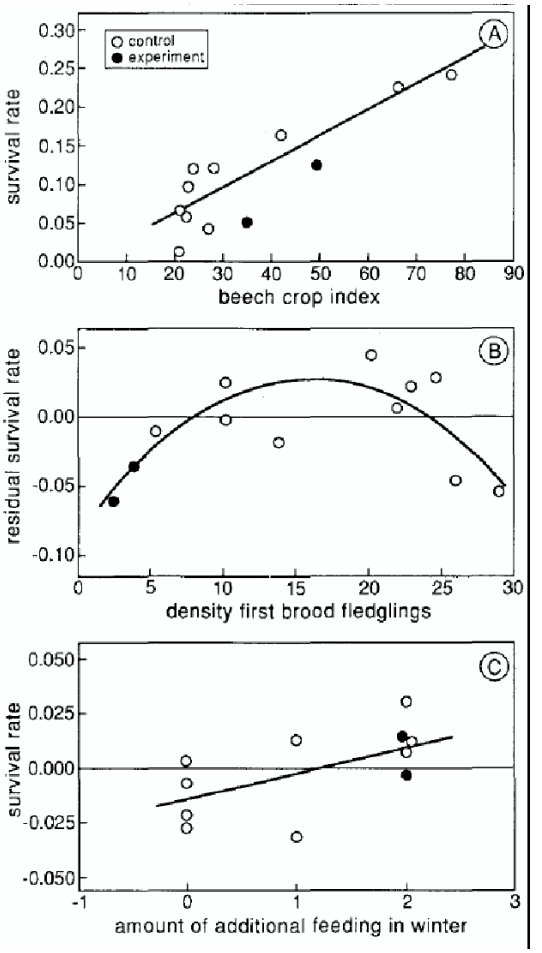

Fig. 1. Annual local survival of first-brood fledglings of control and experimental years. A. plotted against beech-crop index. Regression line is based on control years only. B. Residuals of Fig. 1a plotted against density of first-brood fledglings (fledglings/10 ha). Regression line is based on control years only. C. Residuals of Fig. 1b (calculated using the regression line through both control and experimental years) plotted against the amount of additional feeding in winter (no feeding = 0, small scale feeding = 1, large scale feeding = 2). Although statistical evaluation was based on arcsine transformed data, the figures are based on untransformed data.

Replacement of density of first-brood fledglings by the density of all early fledglings (hatched before 12 June) and the survival of first-brood fledglings by the survival of all early fledglings yielded the same results. Density of second-brood fledglings (or of late fledglings, hatched after 11 June) and density of breeding pairs did not significantly affect local survival rate of first-brood fledglings.

Additional feeding had a positive effect on local survival of first-brood fledglings if the effects of beech crop and density of first-brood fledglings were taken into account (R^2 = 0.96, beech crop: $P < 0.001$, density: $P < 0.001$, density squared: $P < 0.001$, additional feeding: $P < 0.02$, Fig. 1c).

All two-way interactions between variables in the model were tested and none was significant.

Second-brood fledglings

Local survival of second-brood fledglings was positively correlated with beech-crop index (R^2 = 0.40, $P < 0.03$, Fig. 2a). To test whether the density-manipulation affected local survival rate, the experiment was added to this regression model as a dummy variable. Local survival after removal of first brood fledglings was significantly higher than expected on the basis of the beech-crop index (R^2 = 0.69, beech crop: $P < 0.02$, experiment: $P < 0.02$). The dummy variable in the model could be replaced by density of first-brood fledglings (R^2 = 0.83, beech crop: $P < 0.004$, density: $P < 0.002$, Fig. 2b) and subsequent addition of the dummy variable to this model was no longer significant (experiment: $P > 0.3$). This implies that the experiment raised local survival rate of second-brood fledglings as much as expected on the basis of non-experimental data. Density of second-brood fledglings (or of late fledglings, hatched after 11 June), density of breeding pairs and additional feeding in winter did not significantly affect local survival rate of second-brood fledglings. Analysis of local survival of all late fledglings, instead of only second-brood fledglings, yielded the same result. All two-way interactions between variables in the model were tested and none was significant.

The analysis for both first- and second-brood fledglings was repeated with the proportion of

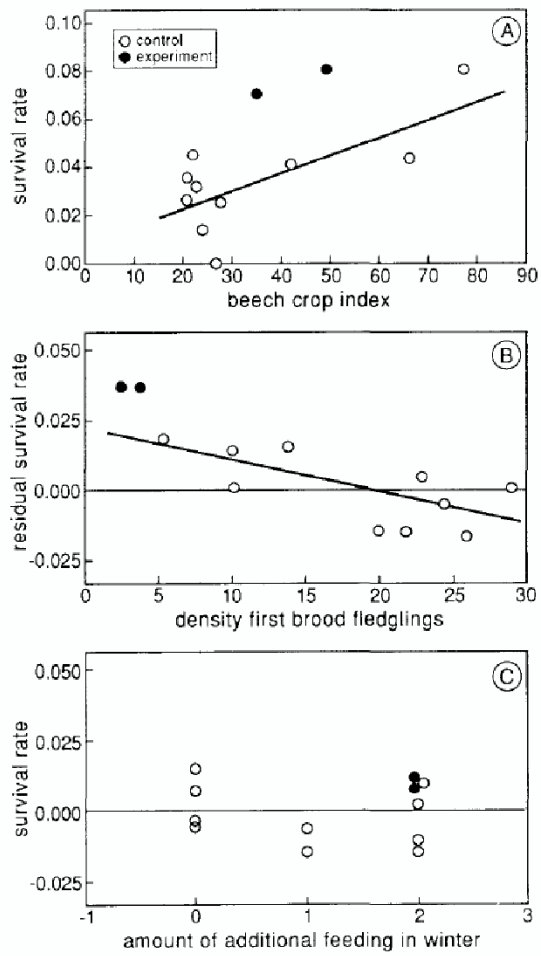

Fig. 2. Local survival of second-brood fledglings. Legend as in Figure 1.

birds recaptured as local recruit in the first year after fledging as dependent variable (instead of all recaptures after 31st of march after the year of hatching). This proportion was corrected for capture rate of breeding birds (Tinbergen *et al.* 1985). These analyses yielded the same results.

DISCUSSION

Beech crop and additional food

Local survival of first- and second-brood fledglings was positively correlated with the beech-crop

index (Fig. 1a & 2a). This is consistent with Van Balen's analysis of approximately the same data (Van Balen 1980) and with results obtained elsewhere (Perrins 1965, Tinbergen *et al.* 1985). Although Great Tits do in fact eat beech seeds when available (Van Balen 1980), it is not clear whether the relationship between seed availability and local survival of tits is causal. Perrins (1965) suggests that differences in survival rate between years with high and low beech crops are already established before the time that tits eat the seeds. A further complication is that local survival is correlated with the beech-crop index in areas without beeches (for example on Vlieland, Tinbergen *et al.* 1985). It is therefore unlikely that the seed crop itself is the sole causal factor involved. For a completer discussion of the subject see Perrins (1965), Van Balen (1980) and Tinbergen *et al.* (1985).

Additional feeding raised local survival of first-brood fledglings (Fig. 1c), but not of second-brood fledglings (Fig. 2c). Although Van Balen (1980) analysed approximately the same set of Hoge Veluwe data, he found no such effect. There are two likely causes for this difference in results. Firstly, Van Balen did not analyse first- and second-brood fledglings separately and secondly, the effect of additional feeding is only significant when the effect of beech crop and the (quadratic) effect of fledgling density is taken into account.

Why is there no effect of additional feeding on second-brood fledglings? The distribution of the additional food (up to six food containers) may have played a role. Second-brood fledglings are subordinate to adults and first-brood fledglings (Drent 1983) and the surrounding territorial birds and first-brood fledglings may have prevented the second-brood fledglings from using the additional food. This idea was originally suggested by Van Balen (1980) to explain why, in his analysis, additional feeding affected survival of adults, but not of juveniles. Reduced access to the food could also be caused by higher dispersal rates of second-brood fledglings (Dhondt & Hublé 1968, Kluyver 1971).

Since additional feeding affected local survival of first-brood fledglings it can be concluded that the availability of food in winter is causally related to local survival of first-brood fledglings. For second-brood fledglings however no conclusion can be reached. I found no effect of additional feeding but I do not know whether the second-brood fledglings had access to the food.

Density dependence

A quadratic relationship was found between density of first-brood fledglings and the local survival rate of these fledglings. This implies that as density increased up to a certain point, local survival rate of first-brood fledglings increased. However, beyond that point, an increase in density lowered local survival rate. The experimental data fit the relationship between local survival of first-brood fledglings and density of first-brood fledglings as deduced from the non-experimental years. This can be seen in Figure 1b in which the experimental data are very close to the regression line although this line is based on control years only. It can therefore be concluded that the (quadratic) relationship between density and local survival rate of first-brood fledglings is causal.

What could be the underlying mechanism of this relationship? The quadratic relationship between density and survival of first-brood fledglings may be the outcome of two independent processes. The probability of being caught by a predator may increase when density becomes very low which would explain the ascending part of the curve. This could be caused by a limited possibility to form flocks when density is low. At very high density increasing competition between fledglings may reduce survival rate, explaining the descending part of the curve. No data are available however to test these hypotheses.

Local survival rate of second-brood fledglings was raised by the removal of first-brood fledglings (Fig. 2a) and this is consistent with predictions based on Kluyver's hypothesis. The data from experimental years fitted the relationship between local survival rate and density of first-brood fledglings as deduced from the non-experimental years (Fig. 2b). I therefore conclude that a causal relationship between density of first-brood fledglings and local survival rate of second-brood fledglings

exists. Furthermore, local survival rate of second-brood fledglings could not be shown to be affected by density of adult birds or density of all late fledglings. Tinbergen *et al.* (1985) came to the same conclusions after his analysis of Kluyver's study on Vlieland.

There is a negative correlation between the occurrence of second clutches and density of breeding pairs (Kluyver 1951). Density dependent survival of second-brood fledglings may provide a functional explanation for this relationship (Tinbergen *et al.* 1985). All other fitness components being independent of density, the density dependent survival of second-brood fledglings leads to a negative relationship between density and the reproductive value of a second clutch. As a result the probability that the optimal behaviour is to start a second clutch will decrease as density increases.

It is a general pattern that there is a seasonal decline in the survival of juvenile birds (Perrins 1970, Daan *et al.* 1989). The effect of first-brood fledglings on local survival of second-brood fledglings can also be interpreted as an effect of birds hatched at the beginning of the season on the survival of birds hatched near the end of the season. Birds fledging early in the season tend to dominate birds fledging later in the season and it has been suggested that this plays an important role in the causal chain underlying the seasonal decline in survival (Kikkawa 1980, Garnett 1981, Drent 1983, Arcese & Smith 1985, Nilsson & Smith 1988). The results presented here support this hypothesis since removal of early fledglings enhanced local survival of late fledglings. This leads me to propose that in species where differential competitive abilities between early and late fledglings plays a role in the causal chain leading to the seasonal decline in juvenile survival the steepness of this decline will be density dependent, with steep declines occurring at high densities. This idea is corroborated by the fact that in one of our study areas density is high (Oosterhout: Van Balen 1973) and there is a strong seasonal decline in juvenile survival within first broods (Verhulst & Tinbergen 1991) while in another study area density is much lower (De Hoge Veluwe: Van Balen 1973) and, within first broods, there is no seasonal decline in juvenile survival (Tinbergen & Daan 1990).

Kluyver (1971) concluded that there was a negative correlation between density of adult birds and local survival rate of fledglings. However, he did not take possible effects of beech crop into account. This may explain his results since it has been shown that a negative relationship exists between density of breeding birds and the size of the beech crop in the following winter (Van Balen & Hage 1989).

It is not known to what extent annual variation in local survival reflects variation in total survival. Young that were not recaptured may have died but may also have emigrated. However, unless emigration is assessed quantitatively as a function of density, there is no way of judging whether this can explain the locally observed density dependent survival effects.

It has been shown that adult density plays a role in territory acquisition in autumn (Tinbergen *et al.* 1987). However, no effect of adult density on fledgling survival is found in this analysis or in the analysis of the data collected on Vlieland (Tinbergen *et al.* 1985), even though there was sufficient variation in adult density in this study (range 3.7 - 10.1 adults / 10 ha, C.V. 34%). This raises the question how important the period of territory acquisition in autumn is as a cause of variation in annual local survival rates of fledglings. The data presented here suggest that other factors, such as beech crop and fledgling density, are quantitatively more important and thereby make the effect of adult density negligible. This idea is supported by the fact that food supply and fledgling density together already explain 96% and 83% of the annual variation in local survival of first- and second-brood fledglings respectively.

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SAMENVATTING

Kluyver voerde een experiment uit om het verband tussen dichtheid en overleving bij juveniele Koolmezen te onderzoeken. Dit experiment bestond uit het manipuleren van de dichtheid van de jongen door in 2 jaar in de Hoge Veluwe eieren en nestjongen uit eerste broedsels te verwijderen. In dit artikel wordt een analyse gepresenteerd van de effecten van dichtheid en voedsel op de lokale overleving van juveniele Koolmezen.

Bij zowel de jongen uit het eerste als bij jongen uit het tweede broedsel was er een sterk verband tussen overleving en de Beukenotenoogst in de winter volgend op het geboortejaar (Fig. 1a & 2a). Bij jongen uit het eerste, maar niet bij tweede broedsel, had bijvoeren in de winter ook een positief effect op de overleving (Fig. 1c & 2c).

Het effect van de dichtheidsmanipulatie verschilde tussen jongen uit eerste broedsels en jongen uit tweede broedsels. Er is een kwadratisch verband tussen de dichtheid van jongen uit het eerste broedsel en de overleving van die jongen. Dat wil zeggen dat met toenemende dichtheid de overleving eerst toeneemt en vervolgens, als een bepaalde dichtheid bereikt is, weer afneemt. De overleving van eerste-broedsel-jongen in jaren waar de dichtheid van eerste-broedsel-jongen gemanipuleerd is, komt overeen met de verwachte overleving op grond van de controle-jaren (Fig. 1b). Dit geeft aan dat er een causaal (kwadratisch) verband bestaat tussen (lokale) overleving en dichtheid. Van de dichtheid van volwassen vogels en de dichtheid van tweede-broedsel-jongen kon niet aangetoond worden dat ze een effekt hadden op de overleving van eerste-broedsel-jongen.

Het experiment had een positief effect op de overleving van de tweede-broedsel-jongen (Fig. 2a). Dit effect was in overeenstemming met de experimentele verandering in dichtheid van de eerste-broedsel-jongen (Fig. 2b). Hieruit concludeer ik dat er ook een causaal verband is tussen de dichtheid van eerste-broedsel-jongen en de (lokale) overleving van tweede-broedsel-jongen. Van de dichtheid van volwassen vogels en de dichtheid tweede-broedsel-jongen kon niet aangetoond worden dat deze factoren invloed hadden op de overleving van de tweede-broedsel-jongen.

Deze studie laat zien dat voedsel en dichtheidsafhankelijke processen een belangrijke rol spelen in de populatiedynamica van de Koolmees.